

Demographic Analysis of Lost River Sucker and Shortnose Sucker Populations in Upper Klamath Lake, Oregon

ERIC C. JANNEY,* RIP S. SHIVELY, BRIAN S. HAYES, AND PATRICK M. BARRY

U.S. Geological Survey, Western Fisheries Research Center, Klamath Falls Field Station,
2795 Anderson Avenue, Suite 106, Klamath Falls, Oregon 97603, USA

DAVID PERKINS

U.S. Fish and Wildlife Service, 300 Westgate Center Drive, Hadley, Massachusetts 01035, USA

Abstract.—We used 13 years (1995–2007) of capture–mark–recapture data to assess population dynamics of endangered Lost River suckers *Deltistes luxatus* and shortnose suckers *Chasmistes brevirostris* in Upper Klamath Lake, Oregon. The Cormack–Jolly–Seber method was used to estimate survival, and information theoretic modeling was used to assess variation due to time, gender, species, and spawning subpopulations. Length data were used to detect multiple year-class failures and events of high recruitment into adult spawning populations. Average annual survival probability was 0.88 for Lost River suckers and 0.76 for shortnose suckers. Mean life span estimates based on these survival rates indicated that Lost River suckers survived long enough on average to attempt reproduction eight times, whereas shortnose suckers only survived to spawn three to four times. Shortnose sucker survival was not only poor in years of fish kills (1995–1997) but also was low in years without fish kills (i.e., 2002 and 2004). This suggests that high mortality occurs in some years but is not necessarily associated with fish kills. Annual survival probabilities were not only different between the two species but also differed between two spawning subpopulations of Lost River suckers. Length composition data indicated that recruitment into spawning populations only occurred intermittently. Populations of both species transitioned from primarily old individuals with little size diversity and consistently poor recruitment in the late 1980s and early 1990s to mostly small, recruit-sized fish by the late 1990s. A better understanding of the factors influencing adult survival and recruitment into spawning populations is needed. Monitoring these vital parameters will provide a quantitative means to evaluate population status and assess the effectiveness of conservation and recovery efforts.

In general, population growth rates in long-lived species with delayed breeding are highly sensitive to temporal variation in survival and are less sensitive to vital rates associated with reproduction (Doherty et al. 2004; Schaub and Pradel 2004). For an animal population to avoid extinction, population growth rates must have a limited amount of temporal variation. Natural selection therefore favors low process variance in characteristics affecting population growth (Pfister 1998). Consequently, it is important to understand temporal variation in survival and to identify different sources of mortality for imperiled animals with this life history strategy. Understanding the causes of variation in survival can help managers to reduce extinction risk, limit population declines, and enhance population growth (Schaub and Pradel 2004).

Lost River suckers *Deltistes luxatus* and shortnose suckers *Chasmistes brevirostris* are long-lived, late-maturing catostomids that are endemic to the Upper Klamath Basin in southern Oregon and northern

California (Scopettone and Vinyard 1991). Historical accounts indicate that both species were once extremely abundant throughout the upper basin and were used in a subsistence fishery by Native Americans and later in a popular recreational snag fishery that was closed in 1987 (Markle and Cooperman 2002). Declining population trends and range reductions were noted for both species as early as the mid-1960s. However, the extent of these declines was not evident until the mid-1980s, when recreational catch rates exhibited dramatic decreases that were attributable in part to overfishing (Markle and Cooperman 2002; NRC 2004). Estimated annual fishery harvest of spawning suckers in the Sprague and Williamson rivers ranged from over 10,000 fish in 1968 to 687 fish in 1985 (Markle and Cooperman 2002). In addition to declining catches, age data from suckers collected during a 1986 fish kill indicated that the Lost River sucker population was composed of very old individuals and that no substantial recruitment had occurred during the previous 15 years (Scopettone and Vinyard 1991; USFWS 1993). These findings led to the federal listing of both species under the Endangered Species Act in 1988 (USFWS 1993). Upper Klamath Lake, Oregon,

* Corresponding author: ejanney@usgs.gov

Received October 23, 2006; accepted May 29, 2008
Published online December 22, 2008

probably contains the largest remaining populations of both species (NRC 2004).

Life history and spawning characteristics of suckers in Upper Klamath Lake are reasonably well understood (Scopetone and Vinyard 1991; Moyle 2002; Cooperman and Markle 2003). Age estimates for Lost River suckers have exceeded 40 years, and most individuals reach maturity between 7 and 9 years. For shortnose suckers, ages greater than 30 years have been estimated, and most individuals reach maturity between 5 and 7 years (NRC 2004). In both species, males typically reach maturity earlier than females. Both species are obligate lake dwellers and typically only leave Upper Klamath Lake to make spawning runs up lake tributaries between March and May of each year. Shortnose suckers primarily spawn in the Williamson and Sprague rivers, but two distinct subpopulations of Lost River suckers have been identified in Upper Klamath Lake (NRC 2004). One subpopulation migrates up the Williamson and Sprague rivers, and the other spawns at several springwater upwelling areas along the eastern shoreline of the lake. Tagging data indicate a high degree of spawning site fidelity and little reproductive mixing between the two subpopulations (U.S. Geological Survey [USGS], unpublished data).

Although fishing mortality was eliminated with the closure of the recreational fishery, poor survival of adult suckers is still thought to be a major factor precluding recovery of Upper Klamath Lake populations (NRC 2004). Upper Klamath Lake has progressed to a hypereutrophic state due to increased nutrient loading from wetland drainage, grazing, and timber harvest (Eilers et al. 2004). These conditions lead to massive blooms of the alga *Aphanizomenon flos-aquae* between June and October of each year (Kann and Smith 1999). The algal blooms and their subsequent die-offs produce water quality conditions that are deleterious to fish health (low dissolved oxygen, high ammonia, and high pH). Poor water quality conditions are thought to have contributed to a number of substantial fish kills in the lake, most recently during summer 1986, 1995, and 1997 (NRC 2004) and to a much lesser extent in summer 2003 (USGS, unpublished data).

Although the two species were listed as endangered in 1988, an understanding of their population dynamics and past and current population status is still lacking. We analyzed 13 years (1995–2007) of capture–mark–recapture data to evaluate trends in adult Lost River sucker and shortnose sucker survival. Annual adult survival probability estimates were modeled and compared to assess differences attributable to species, distinct spawning population segment, gender, and year. In addition to survival, we assessed annual

changes in size composition based on length data collected from spawning populations. Relative change in length frequency was used to provide insight into the relative frequency of recruitment into the adult spawning populations.

Methods

Sampling and fish handling.—Two distinct spawning populations of Lost River suckers were sampled to evaluate and compare annual survival rates. The subpopulation of Lost River suckers that spawns along the eastern shoreline of Upper Klamath Lake was sampled at five known spawning areas using 30-m trammel nets (1.8 m high; two 30-cm-mesh outer panels; one 3.8-cm-mesh inner panel; foam-core float line; lead-core bottom line) between February and May 1995–2007 (Figure 1). Nets were set at each area starting at the shoreline and extended out in a semicircular fashion that encompassed the perimeter of identified spawning areas. The Lost River sucker spawning subpopulation in the Sprague River was sampled at the Chiloquin Dam fish ladder from 2000 to 2007. Before sampling at the fish ladder, a screen was placed over the bottom entrance (outflow) to prevent fish from exiting and the upstream end (inflow) was blocked by a board to lower the water level in the fish ladder. A combination of dip nets and short trammel nets was then used to collect fish trapped in the ladder.

Annual trammel-net sampling for adult shortnose suckers was conducted at numerous sites in Upper Klamath Lake and in the lower Williamson River (Figure 1). Adult shortnose suckers were captured in 100-m trammel nets (all attributes except length were the same as those of the 30-m nets) between February and May 1995–2007. In addition to trammel-net sampling, shortnose suckers were also captured at the Chiloquin Dam fish ladder on the Sprague River from 2000 to 2007. A resistance board weir with a live trap (described in detail by Tobin 1994) was deployed on the Williamson River at river kilometer 10 (Figure 1) in 2005–2007 to improve capture rates of shortnose suckers during spawning migrations. The weir functioned by restricting sucker passage to two weir sections. An upstream live trap was used to capture adult fish as they migrated upriver through the weir, and a downstream trap was used to allow downriver-migrating suckers to pass the weir. High flows in the Williamson River during the majority of the 2006 spawning season, however, inundated the weir and allowed suckers to pass over and around the weir without swimming through the trap.

Suckers captured at all sample locations were identified to species and gender and were scanned for

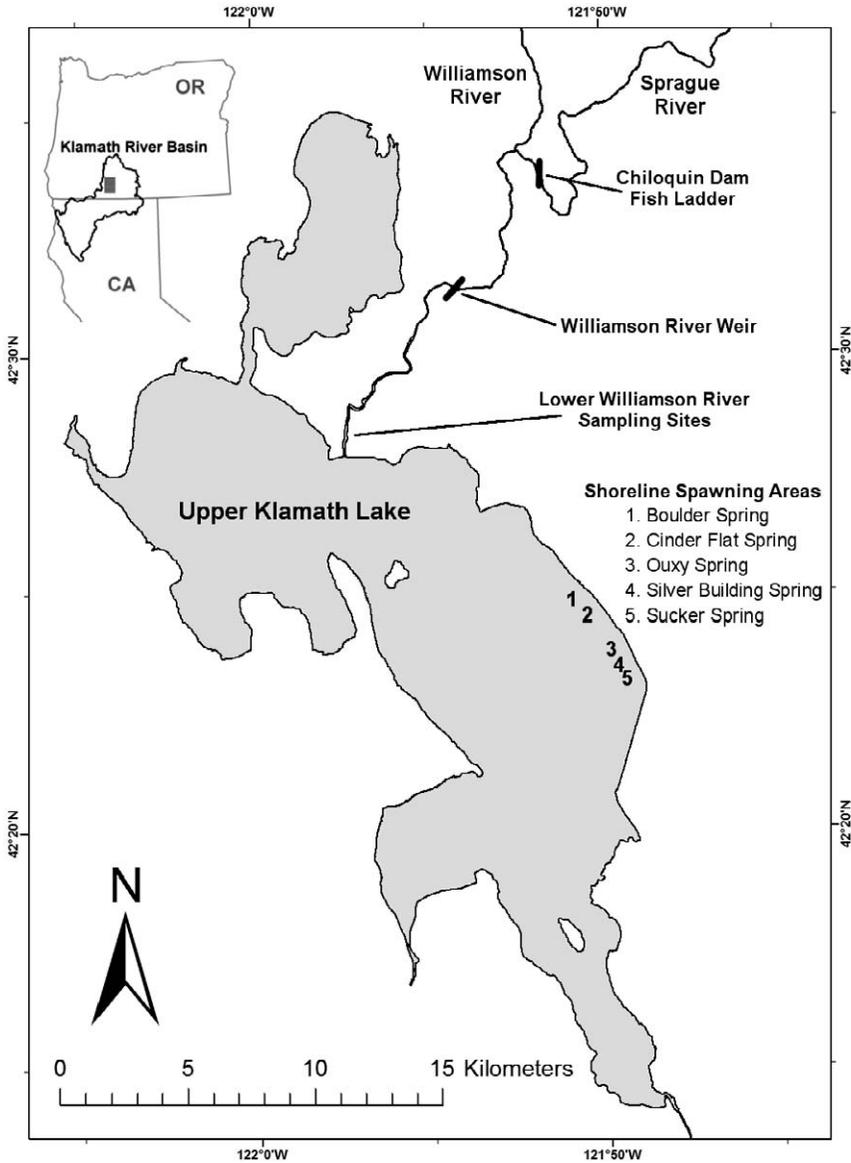


FIGURE 1.—Upper Klamath Lake map, showing U.S. Geological Survey sampling locations for Lost River suckers and shortnose suckers. Inset illustrates the general location of the lake in Oregon.

the presence of a passive integrated transponder (PIT) tag. If a PIT tag was not detected, one was inserted into the abdominal musculature. From 1995 to 2004, suckers were tagged with 125-kHz, full-duplex PIT tags; from 2005 to 2007, fish received 134-kHz, full-duplex tags. All fish were released immediately after being tagged.

Remote PIT tag antenna systems.—In addition to traditional capture techniques (i.e., trammel nets and fish ladder), detections from fixed, underwater PIT tag antennas were incorporated into the capture-mark-

recapture study design beginning in 2005; this was done in an attempt to improve the probability of recapturing previously tagged suckers. Sucker detections by these systems did not involve physical handling of fish; however, the fish were assumed to be alive and thus were counted as live recaptures. Locations of fixed, underwater PIT tag detection systems included the lower Williamson River fish weir (2005–2007), the entrance and exit of the Chiloquin Dam fish ladder (2006–2007), and lakeshore spawning sites (2005–2007).

Survival analysis.—We used a Cormack–Jolly–Seber live-recapture model (Schwarz and Seber 1999) in program MARK (White and Burnham 1999) to obtain maximum likelihood estimates of apparent survival (ϕ_i) and recapture probability (p_i) for adult Lost River suckers and shortnose suckers. Apparent survival is the complement of the sum of mortality and permanent emigration (Pollock et al. 2007). Radiotelemetry studies (USGS, unpublished data) indicate that permanent emigration out of Upper Klamath Lake and its tributaries by either species is uncommon. Therefore, we believe our estimates of ϕ were nearly equivalent to true survival. Lost River sucker data were analyzed separately based upon spawning subpopulations. Lost River sucker capture events in Upper Klamath Lake nonspawning areas were excluded from analysis because the spawning subpopulation membership of those fish could not be ascertained.

Double-tagging data (USGS, unpublished data) indicated that PIT tag loss in suckers was minimal and did not introduce substantial negative bias into ϕ estimates. We assessed whether our data conformed to the assumptions of the Cormack–Jolly–Seber model using goodness-of-fit testing in program UCARE (Choquet et al. 2005). Goodness-of-fit tests pooled over time indicated a significant departure from frequencies expected under the Cormack–Jolly–Seber model for both Lost River sucker subpopulations and for shortnose suckers. Lack of fit can be an indication of model assumption violations, sparse data, or lack of independence. Closer examination of goodness-of-fit tests for individual time periods revealed no consistent or systematic bias that would suggest handling or trapping effects. Lack of fit in our data was probably due to a combination of data sparsity at the beginning of the study and the lack of independence. The lack of independence (i.e., overdispersion) probably results from schooling behavior and is relatively common in capture–mark–recapture studies of schooling fish (Pollock et al. 2007). A quasiliikelihood correction factor (\hat{c}) was estimated from the most general model for each species by use of the median \hat{c} estimation method (Cooch and White 2006; Lost River sucker lakeshore subpopulation $\hat{c} = 1.39$, Lost River sucker Sprague River subpopulation $\hat{c} = 1.98$, shortnose sucker $\hat{c} = 1.61$). These \hat{c} values were applied to the set of considered models to compensate for overdispersion by inflating variance estimates. Variance inflation factors are recommended when heterogeneity is detected, and they support a conservative approach to inference (Anderson et al. 1994).

A number of models were fitted in MARK to data sets for the Lost River sucker lakeshore- and Sprague River-spawning subpopulations and the shortnose

sucker population. The most general model in each set of models allowed for year and sex effects and the year \times sex interaction on ϕ and p . The most general model also incorporated a possible effect of PIT tag type (125 versus 134 kHz) on p for the last 2 years of the study. We hypothesized that differences in recapture probabilities may have existed due to the greater detection distances of 134-kHz tags at remote underwater antennas. Using the most general model as a starting point, models with fewer parameters were constructed by constraining ϕ and p to remain constant across years, sexes, or both. Additive models were also used to reduce parameters and determine whether differences in ϕ and p between the sexes were consistent over time (Pollock et al. 2007). These less parameterized models were used to select a more parsimonious model and to test the effects of time and sex on ϕ .

We used Akaike's information criterion corrected for small-sample bias (AIC_c) and adjusted for overdispersion (i.e., quasiliikelihood AIC_c [$QAIC_c$]; Burnham and Anderson 2002) as a statistical criterion to evaluate the competing models. Akaike weights (w_i) are reported to provide a measure of each model's relative weight or likelihood of being the best model in the set given the data (Burnham and Anderson 2002). Rather than making inference from parameter estimates using only the best model (i.e., that with the smallest $QAIC_c$ value) in the set, predicted parameter estimates were weighted based on model weights. Model-averaged parameter estimates account for model selection uncertainty in the estimated precision of the parameter and thus produce unconditional estimates of variance and standard error (Buckland et al. 1997). A basic random-effects model (Burnham and White 2002) was fitted to the 13 years of recapture data for both the Lost River sucker lakeshore subpopulation and the shortnose sucker population to provide inferences concerning the conceptual population mean annual survival probability ($E[S] = \mu$) and the population or process variance (σ^2) around that mean. Mean life expectancy values conditional upon entry into the adult spawning population were then calculated from the mean ϕ estimate using the methods described by Brownie et al. (1985).

To potentially improve ϕ estimate precision and to evaluate the difference in ϕ between the two sucker species, we conducted a preliminary analysis using recapture data from both species grouped into one data set. We hypothesized that if differences in ϕ between the two species were small or at least consistent, then a more parsimonious model with either no species effect or an additive species effect would be selected and would result in better ϕ estimate precision. Model

TABLE 1.—Akaike’s information criterion corrected for small sample size (AIC_c) and overdispersion (quasilikelihood AIC_c [$QAIC_c$]; overdispersion parameter estimate = 1.39); values were used to select the best model from among 12 candidate models of survival (ϕ) and recapture probability (p) for the lakeshore-spawning subpopulation of Lost River suckers in Upper Klamath Lake, Oregon, 1995–2007 (period symbol = parameter is constant over the given attribute; \times = full model effects; $+$ = additive effects). The best model is presented first; $\Delta QAIC_c$ represents the difference between the $QAIC_c$ value of a model and that of the best model. Akaike weights (w_i) provide a measure of each model’s relative weight or likelihood of being the best model in the set given the data. Number of parameters is the total number that is theoretically estimable by the model.

Model	$QAIC_c$	$\Delta QAIC_c$	w_i	Number of parameters
$\phi(\text{sex} + \text{year}), p(\text{sex} \times \text{year} \times \text{tag type})$	20,714	0.00	0.816	40
$\phi(\text{sex} + \text{year}) p(\text{sex} + \text{year} + \text{tag type})$	20,719	4.27	0.097	26
$\phi(\text{sex} + \text{year}), p(\text{sex} \times \text{year} \times \text{tag type})$	20,720	5.30	0.058	50
$\phi(\text{sex} + \text{year}), p(\text{year} \times \text{tag type})$	20,721	6.61	0.030	28
$\phi(\text{sex year}), p(\text{sex} \times \text{year} \times \text{tag type})$	20,739	24.89	0.000	28
$\phi(\text{sex}), p(\text{sex year tag type})$	20,740	25.20	0.000	39
$\phi(\text{sex year}), p(\text{year} \times \text{tag type})$	20,915	200.79	0.000	38
$\phi(\text{year}), p(\text{year})$	20,926	212.15	0.000	28
$\phi(\text{year}), p(\text{year} \times \text{tag type})$	20,954	239.38	0.000	27
$\phi(\text{year}), p(\text{sex} \times \text{year} \times \text{tag type})$	21,002	288.11	0.000	23
$\phi(\text{sex}), p(\text{sex})$	34,670	13,955.25	0.000	4
$\phi(\cdot), p(\cdot)$	34,743	14,029.09	0.000	2

selection results from this preliminary analysis suggested a strong species effect and indicated that the pooling of data from the two species did not produce a more parsimonious model.

Length composition.—Fork length (FL) of spawning suckers collected from the Williamson and Sprague rivers during 1984–2007 and from lakeshore spawning areas during 1987–2007 were used to visually assess changes in spawner size structure over time. Although this type of length analysis is qualitative in nature, it was useful for observing general trends and detecting multiple year-class failures and relative recruitment into spawning populations (Anderson and Neumann 1996). Length data were grouped annually by species, spawning subpopulation (for Lost River suckers), and sex to avoid size bias resulting from annual changes in species composition and sex ratio. We used age and growth data (USGS, unpublished data) to define the FLs at which the fish typically recruit into the spawning population (Lost River sucker females: <550 mm; Lost River sucker males: <525 mm; shortnose sucker females: <400 mm; shortnose sucker males: <375 mm), but we recognize that some individuals reach sexual maturity at larger sizes. We also recognize that because sucker growth upon attainment of maturity is extremely slow (10–15 mm/year), individuals were probably classified as recruits for multiple years.

Results

Survival Analysis

Between 1995 and 2007, we captured, tagged, and released 3,519 female Lost River suckers and 5,680

male Lost River suckers at lakeshore spawning areas. Of these, we subsequently recaptured or remotely detected 2,489 females and 3,984 males on at least one occasion. Twelve candidate models were fitted to the data for shoreline-spawning Lost River suckers (Table 1). According to $QAIC_c$ values, the best model had additive sex and year effects for ϕ and sex, year, and tag type effects for p . This model accounted for the majority of the model weight (82%) assigned to the candidate models. Model-averaged ϕ estimates varied to some extent by year; female ϕ was consistently, albeit only slightly, higher than male ϕ (Figure 2). Estimate precision was relatively poor from 1995 to 1998 due to low sampling effort but improved substantially in later years as sampling effort increased and remote PIT tag antenna systems became incorporated into the study design. Mean annual survival probability for lakeshore-spawning Lost River suckers from 1995 to 2006 was estimated at 0.88. Based on this estimate, average life expectancy of Lost River suckers upon recruiting into the lakeshore-spawning subpopulation was approximately 8 years. A model with no year effect on ϕ ($\phi[\text{sex}], p[\text{sex} \times \text{year} \times \text{tag type}]$) had a $QAIC_c$ difference ($\Delta QAIC_c$) value of 24.89, indicating that there was virtually no support given the data (Burnham and Anderson 2002). Although model results based on $QAIC_c$ values indicated a strong year effect for ϕ , the process variance over the 12-year period was estimated at only 0.004 (95% confidence interval [CI] = 0.001–0.019).

Between 2000 and 2007, we captured, tagged, and released 5,018 female Lost River suckers and 1,965 males in the Sprague River. Of these, we subsequently

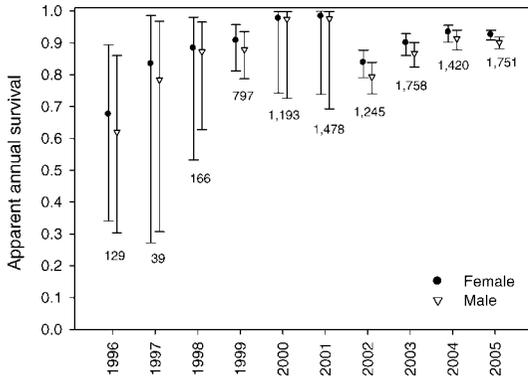


FIGURE 2.—Apparent annual survival probabilities (95% confidence intervals) of male and female Lost River suckers from the lakeshore-spawning subpopulation in Upper Klamath Lake, Oregon, 1996–2005. The number below each estimate indicates the sample size of fish that were captured and released or remotely detected in that year. Estimates for 1995 were on the boundary of 1.0, indicating estimability problems; thus, those estimates are not reported.

recaptured or remotely detected 1,247 females and 708 males on at least one occasion. The structure of the top-ranked model for Sprague River-spawning Lost River suckers was very similar to the one described above for the lakeshore-spawning subpopulation except that the effects of sex, year, and tag type on p were additive (Table 2). This model accounted for 77% of the w_i of candidate models. Survival was estimated on a boundary (1.0) for 2001 and 2005. Boundary estimates can be indicative of estimability problems and were probably a result of sparse recapture data. Because the

reliability of those estimates is questionable, they are not reported (D. R. Anderson, Applied Information Company, personal communication). The model-averaged ϕ estimates varied by year, and female ϕ consistently but slightly exceeded male ϕ . Comparisons of ϕ estimate effect size and 95% CIs between the two subpopulations suggest that ϕ of the Sprague River-spawning segment was substantially lower than that of the lakeshore-spawning segment in 2000, 2002, and 2004 (Figure 3).

Between 1995 and 2004, we captured, tagged, and released 8,156 female shortnose suckers and 5,286 male shortnose suckers. Of these, we subsequently recaptured or remotely detected 3,781 females and 2,034 males on at least one occasion. A total of 12 candidate models were fitted to the shortnose sucker data (Table 3). According to QAIC_c values, the best model had additive sex and year effects for ϕ and year and tag type effects for p . This model accounted for approximately 68% of the w_i in the model set, while the remaining candidate models together accounted for 32% (Table 3). The model-averaged ϕ estimates varied considerably by year; female ϕ was slightly and consistently higher than male ϕ (Figure 4). A model with a sex effect but no year effect on ϕ had a Δ QAIC_c value of 138.8, indicating no support given the data (Burnham and Anderson 2002). Also, process variance around annual ϕ was estimated at 0.045 (95% CI = 0.021–0.146). Estimate precision was relatively poor for several years of data because of the paucity of recaptures. Survival was estimated on a boundary (1.0) for 1998 and 1999; therefore, those estimates are not reported. Estimate precision improved substantially in later years as sampling effort and consistency increased

TABLE 2.—Akaike’s information criterion corrected for small sample size (AIC_c) and overdispersion (quasilikelihood AIC_c [QAIC_c]; overdispersion parameter estimate = 1.98); values were used to select the best model from among 12 candidate models of survival (ϕ) and recapture probability (p) for the Sprague River-spawning subpopulation of Lost River suckers from Upper Klamath Lake, Oregon, 2000–2007 (period symbol = parameter is constant over the given attribute; \times = full model effects; + = additive effects). The best model is presented first; Δ QAIC_c represents the difference between the QAIC_c value of a model and that of the best model. Akaike weights (w_i) provide a measure of each model’s relative weight or likelihood of being the best model in the set given the data. Number of parameters is the total number that is theoretically estimable by the model.

Model	QAIC _c	Δ QAIC _c	w_i	Number of parameters
$\phi(\text{sex} + \text{year}), p(\text{sex} + \text{year} + \text{tag type})$	5,928	0.00	0.770	17
$\phi(\text{sex} + \text{year}), p(\text{sex year} \times \text{tag type})$	5,931	2.93	0.178	19
$\phi(\text{sex} + \text{year}), p(\text{sex} \times \text{year} \times \text{tag type})$	5,933	5.61	0.047	24
$\phi(\text{sex} + \text{year}), p(\text{year} \times \text{tag type})$	5,938	10.26	0.005	17
$\phi(\text{sex year}), p(\text{sex} \times \text{year} \times \text{tag type})$	5,943	15.72	0.000	30
$\phi(\text{sex}), p(\text{sex year tag type})$	5,944	15.94	0.000	12
$\phi(\text{sex year}), p(\text{year} \times \text{tag type})$	5,945	16.89	0.000	22
$\phi(\text{year}), p(\text{year})$	5,946	18.58	0.000	14
$\phi(\text{year}), p(\text{year} \times \text{tag type})$	5,947	19.46	0.000	18
$\phi(\text{year}), p(\text{sex} \times \text{year} \times \text{tag type})$	5,948	20.65	0.000	24
$\phi(\text{sex}), p(\text{sex})$	7,875	1,947.66	0.000	4
$\phi(\cdot), p(\cdot)$	7,877	1,949.57	0.000	2

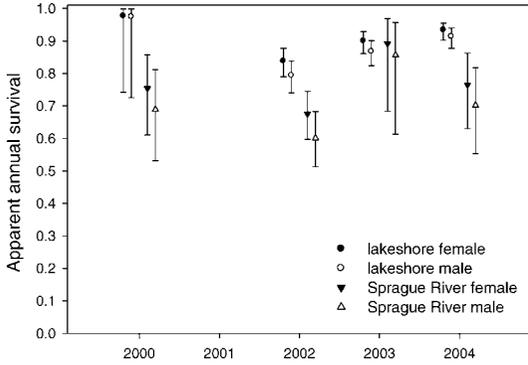


FIGURE 3.—Apparent annual survival probabilities (95% confidence intervals) of male and female Lost River suckers from the Sprague River- and lakeshore-spawning subpopulations of Upper Klamath Lake, Oregon. The 2001 and 2005 Sprague River subpopulation estimates were on the boundary of 1.0, indicating estimability problems; thus, the estimates are not presented.

and underwater PIT tag antennas were incorporated into the study design. Shortnose sucker ϕ was generally lower than Lost River sucker ϕ and was especially low in 1996, 1997, 2001, and 2004. Shortnose sucker mean annual survival probability over the study period was estimated at 0.76. Based on this estimate, average life expectancy of shortnose suckers upon reaching maturity was only 3.6 years.

Length Composition

Major changes in size composition occurred for the lakeshore-spawning subpopulation of Lost River suckers between 1987 and 2007. Length distributions

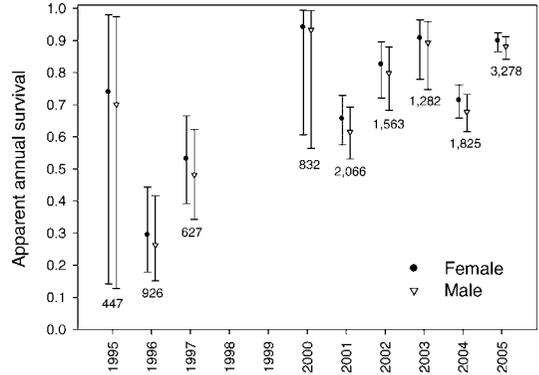


FIGURE 4.—Apparent annual survival rates (95% confidence interval) of male and female shortnose suckers in Upper Klamath Lake, Oregon, between 1995 and 2005. The number below each estimate indicates the sample size of fish that were captured and released or remotely detected in that year. Estimates for 1998 and 1999 were on the boundary of 1.0, indicating estimability problems; thus, those estimates are not reported.

of both males and females indicated that from 1987 to 1991, this subpopulation was mostly composed of large, presumably old fish (Figure 5). Only a small percentage of Lost River suckers captured at lakeshore spawning areas during 1987–1991 were of recruitment size (Figure 6). A shift in size structure occurred in the late 1990s, when a large proportion of Lost River suckers caught at lakeshore spawning sites were observed to be of recruitment size (Figure 6). Also, very few large males were present in catches after 1999. The frequency of large females also decreased substantially in catches from 1999 to 2001. Size

TABLE 3.—Akaike’s information criterion corrected for small sample size (AIC_c) and overdispersion (quasilikelihood AIC_c [$QAIC_c$]; overdispersion parameter estimate = 1.61); values were used to select the best model from among 12 candidate models of survival (ϕ) and recapture probability (p) for shortnose suckers spawning in tributaries of Upper Klamath Lake, Oregon, 1995–2007 (period symbol = parameter is constant over the given attribute; \times = full model effects; $+$ = additive effects). The best model is presented first; $\Delta QAIC_c$ represents the difference between the $QAIC_c$ value of a model and that of the best model. Akaike weights (w_i) provide a measure of each model’s relative weight or likelihood of being the best model in the set given the data. Number of parameters is the total number that is theoretically estimable by the model.

Model	$QAIC_c$	$\Delta QAIC_c$	w_i	Number of parameters
$\phi(\text{sex} + \text{year}), p(\text{year} \times \text{tag type})$	17,950	0.00	0.680	28
$\phi(\text{sex} + \text{year}), p(\text{sex} + \text{year} \times \text{tag type})$	17,952	1.75	0.283	29
$\phi(\text{sex} \times \text{year}), p(\text{year} \times \text{tag type})$	17,956	6.65	0.024	38
$\phi(\text{sex year}), p(\text{sex} \times \text{year} \times \text{tag type})$	17,958	8.54	0.009	40
$\phi(\text{year}), p(\text{sex} \times \text{year} \times \text{tag type})$	17,961	10.89	0.003	39
$\phi(\text{sex} \times \text{year}), p(\text{year} \times \text{year} \times \text{tag type})$	17,969	19.28	0.000	50
$\phi(\text{year}), p(\text{year} \times \text{tag type})$	17,996	46.51	0.000	27
$\phi(\text{sex}), p(\text{sex} \times \text{tag type})$	18,087	136.78	0.000	17
$\phi(\text{sex} + \text{year}), p(\text{sex} + \text{year} + \text{tag type})$	18,101	151.33	0.000	26
$\phi(\text{year}), p(\text{year})$	18,624	674.38	0.000	23
$\phi(\text{sex}), p(\text{sex})$	24,938	6,987.85	0.000	4
$\phi(\cdot), p(\cdot)$	25,010	7,060.28	0.000	2

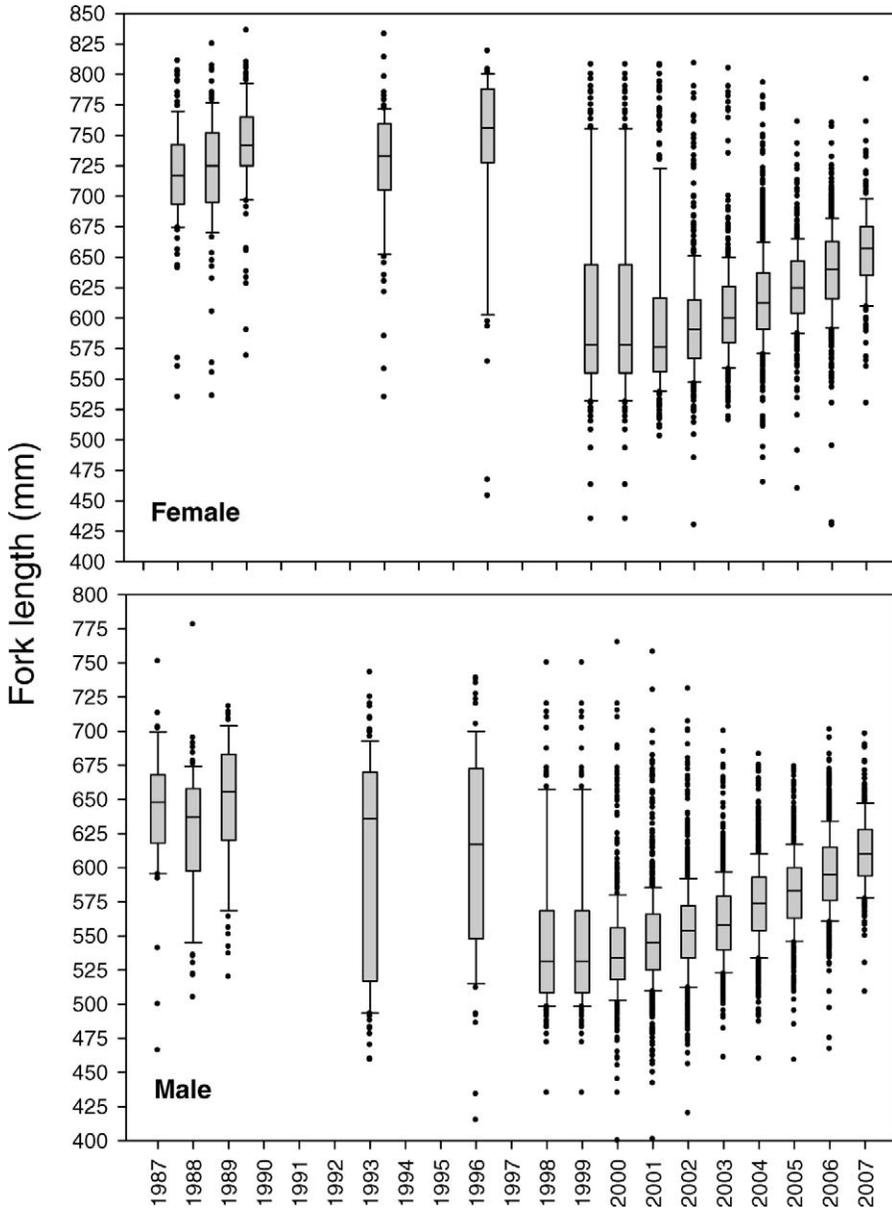


FIGURE 5.—Box-and-whisker plots of the fork lengths (FLs; mm) of male and female Lost River suckers captured at all lakeshore spawning sites in Upper Klamath Lake, Oregon, 1987–2007. Only the first FL measurements are used for fish captured multiple times within a sample season. Lower and upper boundaries of each box correspond to 25th and 75th percentiles, horizontal line in the box corresponds to the median, and whiskers represent 10th and 90th percentiles. Only years in which sample sizes were greater than 50 are presented.

composition for Lost River suckers captured during spawning surveys in the Williamson and Sprague rivers showed a similar shift from very few recruit-sized fish at around the time of endangered species listing to catches dominated by recruit-sized fish in the mid-1990s (Figure 6). A homogeneous size structure and a

slow increase in median FL (10–15-mm/year) were observed in catches of both lakeshore- and river-spawning subpopulations between 2000 and 2007 (Figures 5, 7).

Shortnose suckers sampled in the Sprague and lower Williamson rivers also experienced a substantial

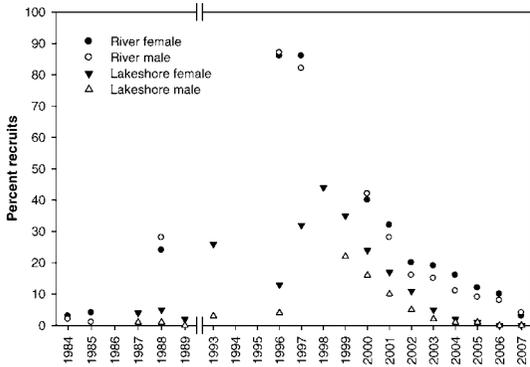


FIGURE 6.—Percentage of recruit-sized Lost River suckers (females < 550 mm fork length [FL], males < 500 mm FL) relative to the number of adults (females > 550 mm FL, males > 500 mm FL) in samples collected from the Sprague and Williamson rivers (river-spawning subpopulation) and from lakeshore spawning areas (lakeshore subpopulation) in Upper Klamath Lake, Oregon. Only years in which sample sizes were greater than 50 are presented.

temporal shift in size composition between 1984 and 2004. Similar to Lost River suckers, shortnose sucker catches in the mid-1980s predominantly consisted of large individuals (Figure 8) but contained few recruit-sized fish (Figure 9). A marked decrease in the size structure of both male and female shortnose suckers occurred in 1995. The majority of individuals captured in 1995 were of recruitment size (Figure 9). A slow increasing trend in shortnose sucker median FL (10–15-mm/year) was observed beginning in 1996 (Figure 8). An exception to this trend occurred in 1999, when some smaller individuals were captured. Similar to the Lost River sucker spawning subpopulations, shortnose suckers exhibited a slowly increasing trend in size and showed little size diversity in recent years (Figure 8).

Discussion

Capture–mark–recapture data from lakeshore-spawning Lost River suckers suggest that except during 1996 and 2002, ϕ rates for this subpopulation were relatively high. Survival rates for 2002 (females = 0.83; males = 0.79) were somewhat low for a long-lived, late-maturing species. It appears that Lost River sucker ϕ was also lower than average in 1996 and 1997; however, poor precision of those estimates limits our ability to assess the effect of the fish kills on the lakeshore-spawning subpopulation. Although model selection results based on QAIC_c indicated a very strong year effect on ϕ , the estimate of process variation (i.e., with sampling variance removed) from a random-effects model suggested relatively little interannual variation. Comparison of effect size and

95% CI between Lost River sucker subpopulations indicated that ϕ was markedly lower for the Sprague River spawners than for lakeshore spawners during 3 of the 4 years in which estimates were available for both. This suggests that although the subpopulations reside together in Upper Klamath Lake for the majority of the year, their population dynamics and status are different. Possible reasons for differences in ϕ between the spawning subpopulations should be investigated in future analyses. If this trend in differential ϕ continues, it may have implications for overall species status determinations and recovery goals.

The overall fitness of the Upper Klamath Lake shortnose sucker population should be of concern given the low observed ϕ and marked temporal variability in ϕ . Model selection results and the process variation estimate from a random-effects model showed considerable interannual variation in adult shortnose sucker ϕ . Our data indicated that shortnose sucker ϕ was not only poor in years of fish kills (i.e., 1995–1997) but was also low in years without observed fish kills (i.e., 2002 and 2004). This suggests that high mortality can occur over a protracted period of time, resulting in poor annual ϕ , but will not necessarily be observed in association with a fish kill. In contrast, water quality conditions during summer 2003 were thought to be especially poor (Wood et al. 2006) and 53 adult Lost River suckers and 29 shortnose suckers were found dead during that summer (USGS, unpublished data). Survival estimates for both sucker species in 2003 indicated that mortality was relatively low. This suggests that small fish kills occur in localized areas but do not necessarily translate to high annual mortality at the population level. Water quality data indicate that poor water quality conditions resulting from massive algal blooms are present every summer (Wood et al. 2005). We do not know why these conditions lead to increased mortality in some years but not other years.

Life history theory and empirical studies of long-lived, late-maturing species have generalized that small changes in adult ϕ can cause large changes in population growth rate for such species (Doherty et al. 2004). Pfister (1998) found that vital rates to which population growth was most sensitive tended to be the least variable over time and least vulnerable to stochastic events. The National Research Council (NRC 2004) recommended that because water quality conditions are unlikely to improve in the near future, recovery actions for sucker populations in Upper Klamath Lake should emphasize measures that maximize production of young fish to offset poor ϕ of adults. However, this management strategy may be ineffective, as population growth for suckers is probably sensitive to

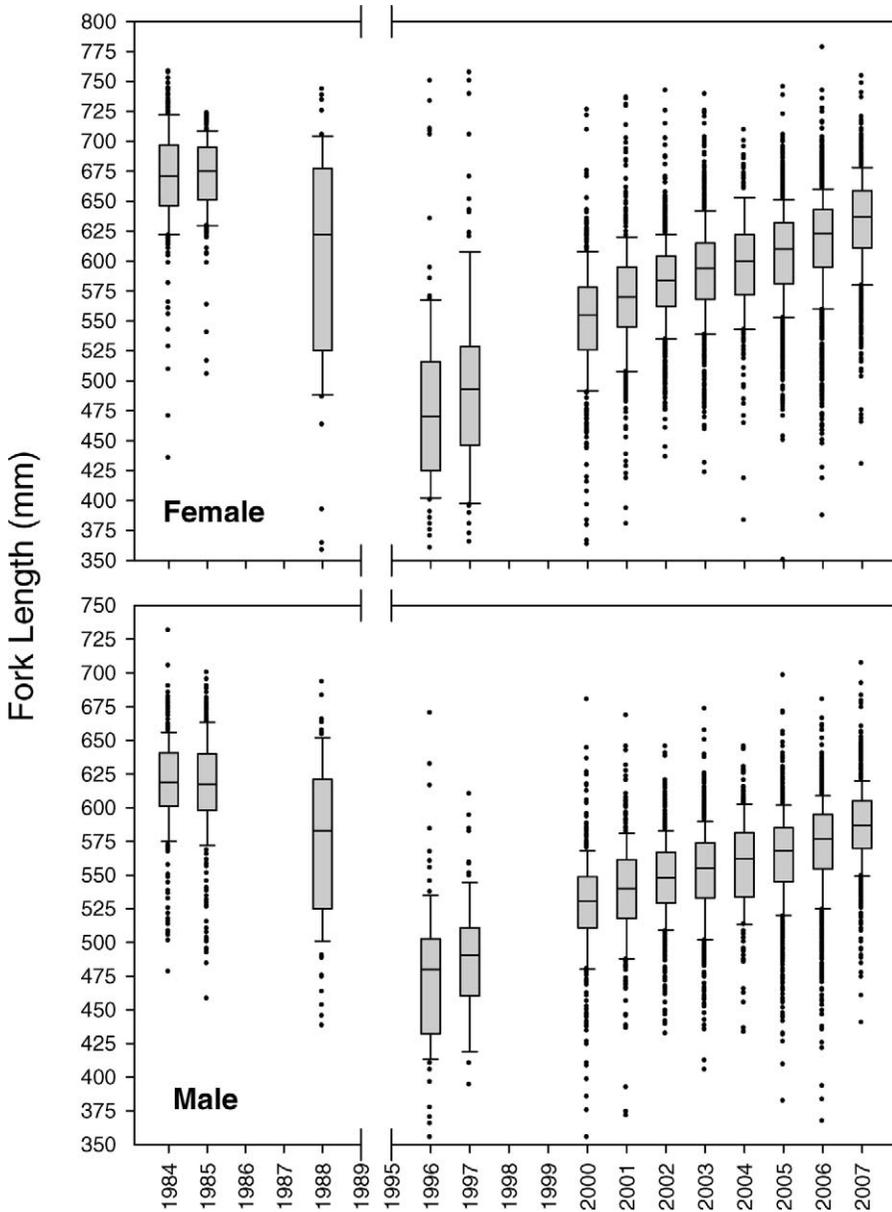


FIGURE 7.—Box-and-whisker plots of the fork lengths (FLs; mm) of male and female Lost River suckers captured in the Williamson and Sprague rivers, Oregon, 1984–2006. Only the first FL measurements were used for fish captured on multiple occasions within a sample season. Lower and upper boundaries of each box correspond to 25th and 75th percentiles, horizontal line in the box corresponds to the median, whiskers represent 10th and 90th percentiles. Only years in which sample sizes were greater than 50 are presented.

adult ϕ and less sensitive to vital rates associated with reproduction (Schaub and Pradel 2004).

Analysis of size structure in Lost River sucker and shortnose sucker populations of Upper Klamath Lake suggests that they have undergone marked demographic changes since being listed as endangered in 1988.

Scoppettone and Vinyard (1991) reported that 95% of the Lost River suckers collected during a 1986 fish kill were between 19 and 30 years old. Lost River sucker FL data collected at shoreline and tributary spawning areas during the late 1980s and early 1990s corroborate the findings of Scoppettone and Vinyard (1991) that at

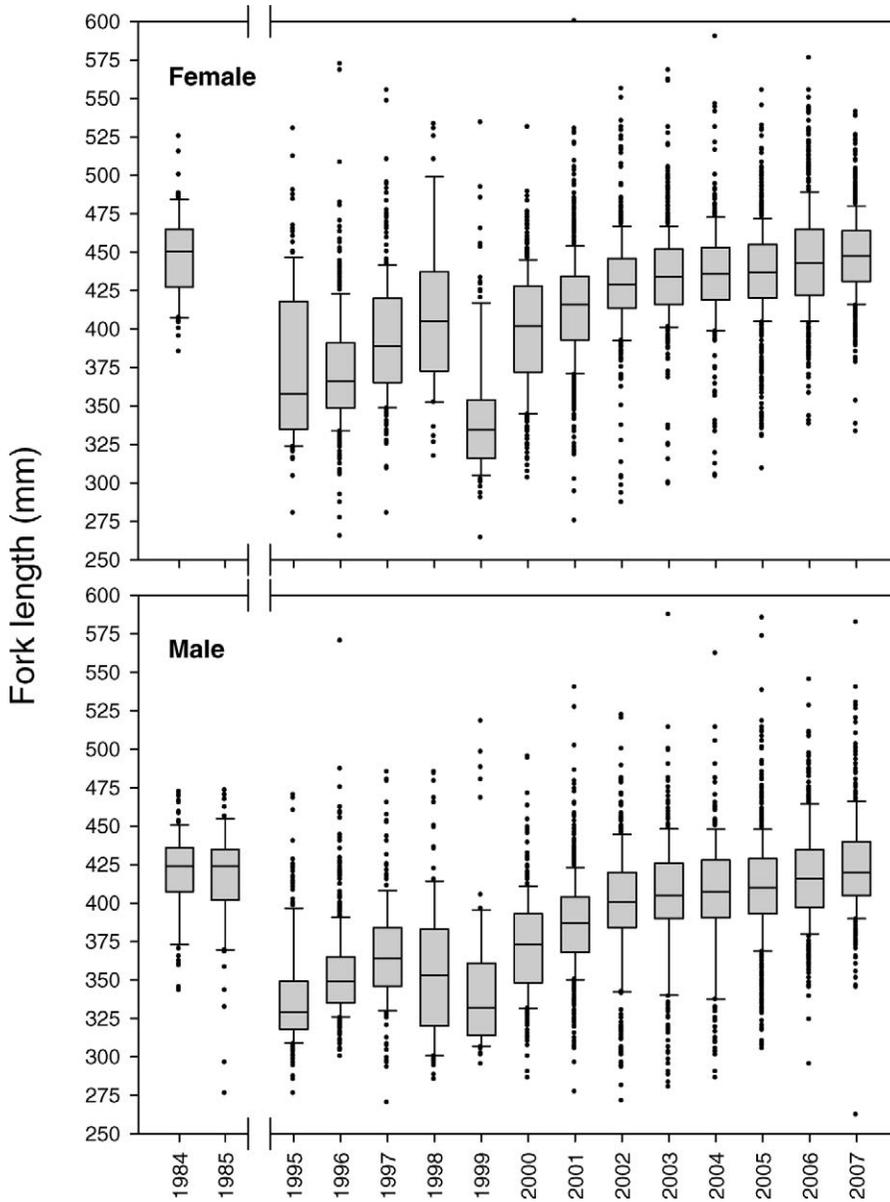


FIGURE 8.—Box-and-whisker plots of the fork lengths (FLs; mm) of male and female shortnose suckers captured in the Williamson and Sprague rivers, Oregon, 1984–2007. Only the first FL measurements were used for fish captured on multiple occasions within a sample season. Lower and upper boundaries of each box correspond to 25th and 75th percentiles, horizontal line in the box corresponds to the median, and whiskers represent 10th and 90th percentiles. Only years in which sample sizes were greater than 50 are presented.

the time of listing, adult Lost River sucker populations contained very old fish and showed no indication of substantial recruitment during the previous 10–15 years. Although little age data existed for shortnose suckers at the time of listing, size data from 1984 and 1985 suggest that this population also consisted of old

individuals and was experiencing a drought in recruitment. Given the empirical age data presented by Scopettone and Vinyard (1991) and the FL data presented here, it is likely that recruitment into adult sucker populations was very low during the 15 years prior to 1988. If annual survival during that time were

similar to rates estimated between 1995 and 2005, Upper Klamath Lake sucker populations were probably depressed at the time of listing.

Populations of both species exhibited a transition from mostly old individuals, little size diversity, and consistently poor recruitment in the late 1980s and early 1990s to primarily small, recruit-sized fish and few large individuals by the late 1990s. This marked shift in size structure to smaller individuals suggests that substantial recruitment into sucker spawning populations occurred sometime during the mid-1990s. The combination of adult mortality and an influx of smaller individuals during the mid-1990s probably explains the rapid decline in relative frequency of large, presumably old individuals. Large female suckers are disproportionately more fecund than are young, recruit-sized females (USGS, unpublished data). Therefore, the absence of large females in spawning populations could potentially reduce population reproductive output (NRC 2004). In recent years, populations of both species have exhibited a slow increase in median FL (10–15-mm/year) and have exhibited little size diversity. This homogeneous size structure suggests that the populations mostly contain similarly aged individuals and that recent recruitment is almost nonexistent.

Future Research

A common difficulty in capture–mark–recapture studies is that parameter estimate precision and effective modeling depend not only upon the number of individuals marked and released but also upon the number that survive and are subsequently captured again (Williams et al. 2002). Due to the sparsity of recapture data, a number of the ϕ estimates from the beginning of this study had wide 95% CIs or were estimated on a boundary and therefore were of limited value. In addition to increases in sampling effort and consistency in 2000, remote underwater PIT tag detection systems were incorporated into the study design in 2005. The use of this relatively new technology improved p by an order of magnitude and dramatically improved the precision of ϕ estimates. These improvements will allow future ϕ analyses to focus on the roles that algal blooms, water quality, disease, and water management play in sucker population dynamics.

It has been suggested that estimates of Upper Klamath Lake sucker abundance are needed to evaluate population status and monitor recovery efforts (NRC 2004). Population estimates derived from capture–recapture data are commonly used to manage fish populations in large systems (e.g., Baker and Borgeson 1999), and population size is a good predictor of extinction risk for endangered animals (O’Grady et al. 2004). We believe, however, that using capture–mark–

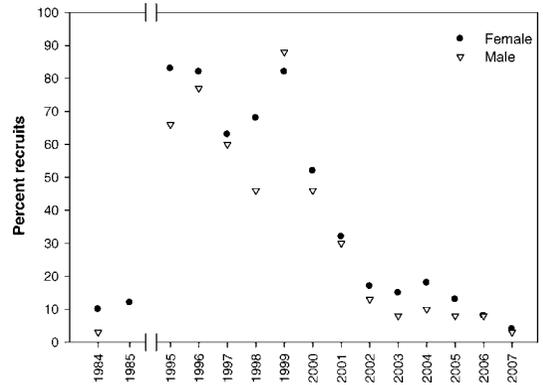


FIGURE 9.—Percentage of recruit-sized shortnose suckers (females < 400 mm fork length [FL], males < 375 mm FL) relative to the number of adults (females > 400 mm FL, males > 375 mm FL) in samples collected from the Sprague and Williamson rivers, Oregon. Only years in which sample sizes were greater than 50 are presented.

recapture methodology to provide such an estimate with a useful level of precision and accuracy would be logistically difficult due to (1) the vast size ($\sim 360 \text{ km}^2$) and openness of Upper Klamath Lake and (2) the heterogeneity in capture probability that was detected in our capture–mark–recapture data (Otis et al. 1978; White et al. 1982; Williams et al. 2002). The consequences of using a poorly derived population estimate with a potentially large bias as the basis for making endangered species and water management decisions could be severe. In addition to annual ϕ , annual rates of population change can be estimated directly from capture–mark–recapture data using the temporal symmetry models described by Pradel (1996) without having to estimate population size. These estimates reflect annual changes in population numbers due to the combined effects of ϕ and recruitment. An advantage of this class of models is that they are substantially less vulnerable to bias caused by model assumption violations (e.g., heterogeneity of capture) than are estimators of population size (Lebreton et al. 1992). Considering the current sampling design and logistical constraints, we feel it is more appropriate to monitor and model population parameters like annual ϕ , recruitment, and rate of population change. A priori modeling of these vital parameters can provide a quantitative means to evaluate the population effects of restoration efforts and to assess environmental factors affecting sucker population dynamics.

Acknowledgments

We are grateful to Gary Scoppettone (USGS, Reno) for his leadership in the early phases of this study.

Greta Blackwood and Alta Scott (USGS, Klamath Falls) oversaw the database and data quality control. David R. Anderson provided invaluable advice concerning data analysis. Lastly, we thank the many persons that worked long hours in adverse conditions to collect data over the course of this study. Part of this work was supported by funds from the U.S. Bureau of Reclamation. Reviews by C. Schwarz, D. Gadomski, T. D. Beard, D. Markle, and M. Wildhaber improved the manuscript. The use of trade, firm, or corporation names in this publication is for the information and convenience of the reader. Such use does not constitute an official endorsement or approval by the U.S. Department of Interior or the USGS of any product or service to the exclusion of others that may be suitable.

References

- Anderson, D. R., K. P. Burnham, and G. C. White. 1994. AIC model selection in overdispersed capture–recapture data. *Ecology* 75:1780–1793.
- Anderson, R. O., and R. M. Neumann. 1996. Length, weight, and associated structural indices. Pages 447–482 in B. R. Murphy and D. W. Willis, editors. *Fisheries techniques*, 2nd edition. American Fisheries Society, Bethesda, Maryland.
- Baker, E. A., and D. J. Borgeson. 1999. Lake sturgeon abundance and harvest in Black Lake, Michigan, 1975–1999. *North American Journal of Fisheries Management* 19:881–1155.
- Brownie, C., D. R. Anderson, K. P. Burnham, and D. R. Robson. 1985. *Statistical inference from band recovery data: a handbook*, 2nd edition. U.S. Fish and Wildlife Service Resource Publication 156.
- Buckland, S. T., K. P. Burnham, and N. H. Agustin. Model selection: an integral part of inference. *Biometrics* 53:603–618.
- Burnham, K. P., and D. R. Anderson. 2002. *Model selection and inference: a practical information theoretic approach*. Springer-Verlag, New York.
- Burnham, K. P., and G. C. White. 2002. Evaluation of some random effects methodology applicable to bird ringing data. *Journal of Applied Statistics* 29:245–264.
- Choquet, R., A. M. Reboulet, J. D. Lebreton, O. Gimenez, and R. Pradel. 2005. U-CARE 2.2 user's manual. Centre D'Ecologie Fonctionnelle et Evolutive, Montpellier, France.
- Cooch, E., and G. C. White. 2006. *Using MARK: a gentle introduction*, 5th edition. Cornell University, New York.
- Cooperman, M. S., and D. F. Markle. 2003. Rapid out-migration of Lost River and shortnose sucker larvae from in-river spawning beds to in-lake rearing grounds. *Transactions of the American Fisheries Society* 132:1138–1153.
- Doherty, P. F., E. A. Schreiber, J. D. Nichols, J. E. Hines, W. A. Link, G. A. Schenk, and R. W. Schreiber. 2004. Testing life history predictions in a long-lived seabird: a population matrix approach with improved parameter estimation. *Oikos* 105:606–618.
- Eilers, J. M., J. Kann, J. Cornett, K. Moser, and A. St. Amand. 2004. Paleolimnological evidence of change in a shallow, hypereutrophic lake-upper Klamath Lake, Oregon, USA. *Hydrobiologia* 520:7–18.
- Kann, J., and V. H. Smith. 1999. Estimating the probability of exceeding elevated pH values critical to fish populations in a hypereutrophic lake. *Canadian Journal of Fisheries and Aquatic Sciences* 56:2262–2270.
- Lebreton, J. D., K. P. Burnham, J. Clobert, and D. R. Anderson. 1992. Modelling survival and testing biological hypotheses using marked animals: a unified approach with case studies. *Ecological Monographs* 62:67–118.
- Markle, D. F., and M. Cooperman. 2002. Relationship between Lost River and shortnose sucker biology and management of upper Klamath Lake. Pages 93–117 in B. Braunworth and T. Welch, editors. *The 2001 water allocation decisions in the Klamath basin*. Oregon State University Extension Publication, Corvallis.
- Moyle, P. B. 2002. *Inland fishes of California*. University of California Press, Berkeley.
- NRC (National Research Council). 2004. *Endangered and threatened fishes in the Klamath River basin*. National Academy Press, Washington, D.C.
- O'Grady, J. J., D. H. Reed, B. W. Brook, and R. Frankham. 2004. What are the best correlates of predicted extinction risk? *Biological Conservation* 118:513–520.
- Otis, D. L., K. P. Burnham, G. C. White, and D. R. Anderson. 1978. *Statistical inference from capture data on closed animal populations*. Wildlife Monographs 62.
- Pfister, C. A. 1998. Patterns of variance in stage-structured populations: evolutionary predictions and ecological implications. *Proceedings of the National Academy of Sciences of the United States of America* 95:213–218.
- Pollock, K. H., J. Yoshizaki, M. C. Fabrizio, and S. T. Schram. 2007. Factors affecting survival rates of a recovering lake trout population estimated by mark–recapture in Lake Superior, 1969–1996. *Transactions of the American Fisheries Society* 136:185–194.
- Pradel, R. 1996. Utilization of capture–mark–recapture for the study of recruitment and population growth rate. *Biometrics* 52:703–709.
- Schaub, M., and R. Pradel. 2004. Assessing the relative importance of different sources of mortality from recoveries of marked animals. *Ecology* 85:930–938.
- Schwarz, C. J., and G. A. F. Seber. 1999. Estimating animal abundance: review III. *Statistical Science* 14:427–456.
- Scoppetone, G. G., and G. Vinyard. 1991. Life history and management of four endangered lacustrine suckers. Pages 359–377 in W. L. Minckley and J. E. Deacon, editors. *Battle against extinction: native fish management in the American West*. University of Arizona Press, Tucson.
- Tobin, J. H. 1994. Construction and performance of a portable resistance board weir for counting migrating adult salmon in rivers. U.S. Fish and Wildlife Service, Kenai Fishery Resource Office, Alaska Fisheries Technical Report Number 22, Kenai.
- USFWS (U.S. Fish and Wildlife Service). 1993. *Lost River (*Deltistes luxatus*) and shortnose (*Chasmistes brevirostris*) sucker recovery plan*. USFWS, Portland, Oregon.
- White, G. C., D. R. Anderson, K. P. Burnham, and D. L. Otis.

1982. Capture–recapture and removal methods for sampling closed populations. Los Alamos National Laboratory, LA-8787-NERP, Los Alamos, New Mexico.
- White, G. C., and K. P. Burnham. 1999. Program MARK: survival rate estimation from both live and dead encounters. *Bird Study* 46(Supplement):S120–S139.
- Williams, B. K., J. D. Nichols, and M. J. Conroy. 2002. Analysis and management of animal populations: modeling, estimation, and decision making. Academic Press, New York.
- Wood, T. M., G. R. Hoilman, and M. K. Lindenberg. 2005. Water-quality conditions in upper Klamath Lake, Oregon, 2002–2004. U.S. Geological Survey Scientific Investigations Report 2006–5209.

ERRATA

Please make the following corrections in a recent issue of this journal.

Volume 137(6), November 2008: “Demographic Analysis of Lost River Sucker and Shortnose Sucker Populations in Upper Klamath Lake, Oregon,” by Eric C. Janney, Rip S. Shively, Brian S. Hayes, Patrick M. Barry, and David Perkins, pages 1812–1825.

Pages 1816–1818. Tables 1, 2, and 3 should be replaced by the following tables:

TABLE 1.—Akaike’s information criterion corrected for small sample size (AIC_c) and overdispersion (quasilikelihood AIC_c [$QAIC_c$]; overdispersion parameter estimate = 1.39); values were used to select the best model from among 12 candidate models of survival (ϕ) and recapture probability (p) for the lakeshore-spawning subpopulation of Lost River suckers in Upper Klamath Lake, Oregon, 1995–2007 (period symbol = parameter is constant over the given attribute; \times = full model effects; + = additive effects). The best model is presented first; $\Delta QAIC_c$ represents the difference between the $QAIC_c$ value of a model and that of the best model. Akaike weights (w_i) provide a measure of each model’s relative weight or likelihood of being the best model in the set given the data. Number of parameters is the total number that is theoretically estimable by the model.

Model	$QAIC_c$	$\Delta QAIC_c$	w_i	Number of parameters
$\phi(\text{sex} + \text{year}), p(\text{sex} \times \text{year} \times \text{tag type})$	20,714	0.00	0.816	40
$\phi(\text{sex} + \text{year}), p(\text{sex} + \text{year} + \text{tag type})$	20,719	4.27	0.097	26
$\phi(\text{sex} \times \text{year}), p(\text{sex} \times \text{year} \times \text{tag type})$	20,720	5.30	0.058	50
$\phi(\text{sex} + \text{year}), p(\text{sex} + \text{year} \times \text{tag type})$	20,721	6.61	0.030	28
$\phi(\text{sex}), p(\text{sex} \times \text{year} \times \text{tag type})$	20,739	24.89	0.000	28
$\phi(\text{year}), p(\text{sex} \times \text{year} \times \text{tag type})$	20,740	25.20	0.000	39
$\phi(\text{sex} \times \text{year}), p(\text{year} \times \text{tag type})$	20,915	200.79	0.000	38
$\phi(\text{sex} + \text{year}), p(\text{year} \times \text{tag type})$	20,926	212.15	0.000	28
$\phi(\text{year}), p(\text{year} \times \text{tag type})$	20,954	239.38	0.000	27
$\phi(\text{year}), p(\text{year})$	21,002	288.11	0.000	23
$\phi(\text{sex}), p(\text{sex})$	34,670	13,955.25	0.000	4
$\phi(\cdot), p(\cdot)$	34,743	14,029.09	0.000	2

TABLE 2.—Akaike’s information criterion corrected for small sample size (AIC_c) and overdispersion (quasilikelihood AIC_c [$QAIC_c$]; overdispersion parameter estimate = 1.98); values were used to select the best model from among 12 candidate models of survival (ϕ) and recapture probability (p) for the Sprague River-spawning subpopulation of Lost River suckers from Upper Klamath Lake, Oregon, 2000–2007 (period symbol = parameter is constant over the given attribute; \times = full model effects; + = additive effects). The best model is presented first; $\Delta QAIC_c$ represents the difference between the $QAIC_c$ value of a model and that of the best model. Akaike weights (w_i) provide a measure of each model’s relative weight or likelihood of being the best model in the set given the data. Number of parameters is the total number that is theoretically estimable by the model.

Model	$QAIC_c$	$\Delta QAIC_c$	w_i	Number of parameters
$\phi(\text{sex} + \text{year}), p(\text{sex} + \text{year} + \text{tag type})$	5,928	0.00	0.770	17
$\phi(\text{sex} + \text{year}), p(\text{sex} + \text{year} \times \text{tag type})$	5,931	2.93	0.178	19
$\phi(\text{sex} + \text{year}), p(\text{sex} \times \text{year} \times \text{tag type})$	5,933	5.61	0.047	24
$\phi(\text{sex} + \text{year}), p(\text{year} \times \text{tag type})$	5,938	10.26	0.005	17
$\phi(\text{sex} \times \text{year}), p(\text{sex} \times \text{year} \times \text{tag type})$	5,943	15.72	0.000	30
$\phi(\text{sex}), p(\text{sex} + \text{year} + \text{tag type})$	5,944	15.94	0.000	12
$\phi(\text{sex} \times \text{year}), p(\text{year} \times \text{tag type})$	5,945	16.89	0.000	22
$\phi(\text{year}), p(\text{year})$	5,946	18.58	0.000	14
$\phi(\text{year}), p(\text{year} \times \text{tag type})$	5,947	19.46	0.000	18
$\phi(\text{year}), p(\text{sex} \times \text{year} \times \text{tag type})$	5,948	20.65	0.000	24
$\phi(\text{sex}), p(\text{sex})$	7,875	1,947.66	0.000	4
$\phi(\cdot), p(\cdot)$	7,877	1,949.57	0.000	2

TABLE 3.—Akaike's information criterion corrected for small sample size (AIC_c) and overdispersion (quasilikelihood AIC_c [$QAIC_c$]; overdispersion parameter estimate = 1.61); values were used to select the best model from among 12 candidate models of survival (ϕ) and recapture probability (p) for shortnose suckers spawning in tributaries of Upper Klamath Lake, Oregon, 1995–2007 (period symbol = parameter is constant over the given attribute; \times = full model effects; $+$ = additive effects). The best model is presented first; $\Delta QAIC_c$ represents the difference between the $QAIC_c$ value of a model and that of the best model. Akaike weights (w_i) provide a measure of each model's relative weight or likelihood of being the best model in the set given the data. Number of parameters is the total number that is theoretically estimable by the model.

Model	$QAIC_c$	$\Delta QAIC_c$	w_i	Number of parameters
$\phi(\text{sex} + \text{year}), p(\text{year} \times \text{tag type})$	17,950	0.00	0.680	28
$\phi(\text{sex} + \text{year}), p(\text{sex} + \text{year} \times \text{tag type})$	17,952	1.75	0.283	29
$\phi(\text{sex} \times \text{year}), p(\text{year} \times \text{tag type})$	17,956	6.65	0.024	38
$\phi(\text{sex} \times \text{year}), p(\text{sex} \times \text{year} \times \text{tag type})$	17,958	8.54	0.009	40
$\phi(\text{year}), p(\text{sex} \times \text{year} \times \text{tag type})$	17,961	10.89	0.003	39
$\phi(\text{sex} \times \text{year}), p(\text{sex} \times \text{year} \times \text{tag type})$	17,969	19.28	0.000	50
$\phi(\text{year}), p(\text{year} \times \text{tag type})$	17,996	46.51	0.000	27
$\phi(\text{sex}), p(\text{year} \times \text{tag type})$	18,087	136.78	0.000	17
$\phi(\text{sex} + \text{year}), p(\text{sex} + \text{year} + \text{tag type})$	18,101	151.33	0.000	26
$\phi(\text{year}), p(\text{year})$	18,624	674.38	0.000	23
$\phi(\text{sex}), p(\text{sex})$	24,938	6,987.85	0.000	4
$\phi(\cdot), p(\cdot)$	25,010	7,060.28	0.000	2